A MODERN REVIEW OF THE DEMISE OF APORIA CRATAEGI L.: THE BLACK-VEINED WHITE

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INTRODUCTIONS AND BREEDING

Experts disagree as to whether or not the butterfly was successfully introduced into Kent during the 1880s, the native insect having been thought by some to have just previously died out; Tutt (1896) and Allan (*loc. cit.*) thought our butterfly extinct since about 1880, whilst Frohawk (1914), Bretherton (1951) and other modern analysts believe it survived naturally as a breeding species until around 1925. The comparatively low September rainfall after 1887 supports the more recent view.

According to Merrifield (1893), a Mr. Edmonds of Windsor had for some years imported the species and allowed numbers to escape, but they had never "taken" until offspring were noticed flying in 1892; the insect successfully colonised the spot until at least the larval stage of spring 1894. September 1891 was roughly average for rainfall, the following season enjoyed 137% of average, and the following two seasons less than usual. Tutt (1896b) overwintered some German larvae during the 1895/96 winter and was "astonished at the great death rate"; only 5-10% survived and the relevant September was a very dry one. In 1903, Frohawk (loc. cit.) tried to breed the species from locally caught examples, but all died "during hibernation"; national rainfall that September averaged 151% of normal, although this did not prevent a local abundance in Kent. He repeated the experiment the following season, with some success, when rainfall was less than average. More modernly, between 1930 and 1940 according to Newman (1954), the insect was for a time successfully re-established near Sandwich with continental stock; unfortunately more precise information is lacking. In the autumn of 1948 and the spring of the following year Newman tried again, with continental larvae being released in Winston Churchill's garden at Chartwell, Kent. This resulted in complete failure "after the hungry tits had been on their rounds in the early morning", as they apparently ate all the pupae (Newman, loc. cit.). More than half a century earlier, Tutt (1896a) mentioned that "larvae have pupated well in some of these instances we know, but the specimens appear to have utterly failed to establish themselves", with a few odd exceptions. More recently, Newman (1965) again reported that the butterfly was breeding in east Kent, in 1964; little further information is available on the occurrence although he did note that other personal attempts at

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re-introduction with German larvae on the North Downs of Kent had been unsuccessful owing to birds eating both larvae and pupae.

In modern times, P. W. Cribb and A. Waters have successfully bred the species in this country from continental stock over several generations, but only by overwintering the larvae under the drier artificial conditions within an unheated greehouse. Large losses were incurred when larvae were sleeved outside, although this should have eliminated most predators. Mortalities occurred mainly during spring and were thought to be due to fungal infection; significantly, deaths were not avoided when larvae originally placed outside were withdrawn to greenhouse conditions at this time. Further small losses were also experienced owing to the parasite Apanteles glomeratus, to predatory insects and to birds eating dispersed larvae. Hundreds of specimens were released on Holmwood Common, Surrey in the mid 1970s but none could be seen during the following season. This recent work strongly supports the view that conditions in England are still not suitable for continental examples of the black-veined white. In Scotland, however, success has been achieved with a colony over the last few years. In 1974 stock from a few hundred Spanish ova began to be reared outside in Fife by Elliott (1977). The next season saw about 200 butterflies successfully emerge and the following year about 100. This artificially assisted introduction has continued, with reinforcements from Swiss/Italian border stock in 1978, more or less successfully until the present time (Elliott, 1982). The colony was shielded from insectivorous birds in 1981 and a 65% survival rate was thereby attained. Over these years a few of the noted losses were due to Apanteles glomeratus but adult butterflies were "very often heavily persecuted by local birds a blackbird, a song-thrush and a great tit".

The evidence presented overall by the general lack of success of foreign introductions and some artificial native rearing is inconsistent with a single causal factor; in the absence of relevant, and intimate, environmental and other recorded data made when our native butterfly was reared in the distant past, any inferences drawn from success or failure are inconclusive, except to say that several elements apparently played a part.

Ford (*loc. cit.*) thought that the black-veined white and some other native species could "only survive by adapting themselves closely to the environment which they find in certain places which chance to suit them particularly well". This could indicate that in addition to the problems already being encountered by our own *A. crataegi*, foreign imports endured an increased difficulty in finding, and then adapting to, a favourable environment in our country.

AVIAN PREDATION

As was mentioned earlier, birds were sometimes blamed for the disappearance of the butterfly in question; Dale (1887) thought the

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decline "due to the great increase of small birds" after their protection. Allan (loc. cit.) said that there "was undoubtedly a rise in the population of many species of our smaller birds suring the 19th century", which was precipitated by the decline of raptorial birds brought about by increased efficiency in game preservation, in turn made possible by several technical advances in the shot-gun: there was no such change on the Continent. The periods of abundance of the blackveined white do not correlate with those times when severe winters were known to have caused heavy mortality amongst insectivorous birds, although it may be of importance that sparrows did not substantially decrease in numbers during the severe winters of 1878 to 1881 (Gurney & Russell, 1885). Nevertheless, Kollar (loc. cit.), writing of larvae, stated that "small birds, particularly the titmice, devour them soon after they are hatched, as well as in the following spring So eager are the birds in the pursuit of these caterpillars, that they break into their nests late in the autumn" in central European colonies. Martelli (loc. cit.) makes a similar assertion. More recently in this country, Newman (1965) noted of several introductions that "larvae steadily diminished in numbers; so obviously some birds, probably tits, were taking them. The same thing happened to the chrysalids". He also noted that of 300 or so larvae he had put on a hedge, only three survived to become butterflies owing to predations by birds and parasites.

The Tit family is probably foremost among birds for initiating new and adaptive feeding habits; whilst there is no evidence that the group changed its predatory habits towards A. crataegi larvae during the 19th century (although it would probably have gone unnoticed), "it is certainly true that the tits may take relatively large proportions of their prey when the prey is not exceptionally abundant" (Perrins, 1979). The long-tailed tit is almost wholly insectivorous and during autumn feeds primarily among hawthorn twigs, spending more than 30% of its time around this feeding site; similarly the great tit spends up to 19% of its time on hawthorn during the months of September and May (Perrins, loc. cit.). In illustration of their efficiency as predators, several other species of tit prey on the early stages of the tiny eucosmid moth Cydia coni*colana* Heyl. and can eat more than half of the available pupae (Gibb, 1958). In Germany at least, titmice attacked larvae of A. crataegi during the cold season and locally accounted for between 70% and 80% (Stellwaag, 1924).

Martelli (*loc. cit.*), reporting from Italy during the late 1920s, noted that sparrows ate many black-veined white pupae and that unclassified birds were also recorded as taking up to 4% of larvae in Russia. As regards the house sparrow in this country, although the bird could be found all over the British Isles by the end of the 17th century (this not having been the case previously), the period up to 1800 was one of consolidation (Summers-Smith, 1963). An extension of numbered range was noted here after that time, following the increase in human population and wheat production, and coincidentally with the decline of *A. crataegi*; locally, by the 1880s a position had been reached such that "sixpence per dozen

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heads of sparrows (until the end of March) will be given to anyone producing them" (Gurney & Russell, *loc. cit.*).

In fruit-growing areas "the sparrow does a fair proportion of good" and in "exceptional cases large numbers of insect pests may be taken by sparrows to feed their young", up to 40% of a nestling's diet being lepidopterous larvae (Summers-Smith, *loc. cit.*). Attacks by birds on adult white butterflies (*Pieris* spp.) have been frequently recorded; Collenette (1935) listed 26 published records of the house sparrow attempting to catch such insects, the sparrow being the foremost bird recorded for assaults on butterflies in this country.

So although there is no proof that birds were solely responsible for the decline of *A. crataegi*, there is plain evidence for their involvement at a significant level.

DISEASES

The mode of the butterfly's disappearance, both locally and nationally, could be described as typical of a disease epidemic and Franz (1971), writing from Germany, considered *A. crataegi* to be a species which undergoes "more or less cyclic gradations regularly terminated by epizootics". Martelli (*loc. cit.*) discusses in detail the causes of death in the black-veined white in Italy during the late 1920s. Three diseases were major mortality factors – the virus-associated "la flaccidezza" and "giallume", and the protozoan infection "pebrin". However, there was no report of diseased larvae being found in Britain at the time of the insect's decline, despite the fact that diseases are the largest single cause of death in insects in general and their significance had been known since the early 19th century.

Fungi

Leatherdale (1958) listed 33 species of fungi which were known to attack lepidoptera in Britain and Madelin (1968) noted that "fungous diseases of insects are both common and widespread, and sometimes are severe enough almost to eliminate a population of insects in a given habitat"; it is "for many sorts of insect the major maortality factor" although this is "usually only one of a number of factors limiting their numbers". The scale of destruction was considerable in Finland, for example, during the autumns of 1928, 1936 and 1939, when *P. brassicae* L. larvae were attacked by the fungus *Entomophthora sphaerosperma* F., and during "many an autumn" this was the most important cause of disease (Kanervo, 1946).

Past objections to the theory that disease caused the disappearance of the black-veined white mainly rested on how such a disease could affect many isolated colonies at about the same time. This objection was first overcome by Steinhaus (1954), who wrote that "spores of certain entomogenous fungi may be continuously present in large numbers in fields ready to attack susceptible insect hosts, but these spores may remain inactive until appropriate con-

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ditions of temperature and humidity prevail"; these fungi would then "spring up abundantly and simultaneously in widely separated localities" with "catastrophic rapidity and thoroughness". Tanada (1964), Franz (*loc. cit.*) and Christensen (1972) concurred with this view. In many colonies the decline of *A. crataegi* was nothing if not quick and absolute (Jenner Weir, 1887).

Most insect diseases are affected by humidity and temperature, but none is more dependent on the former than fungi. "Most entomogenous fungi attack their host through the integument, requiring adequate external humidity or moisture to carry out the process. Most bacteria, viruses and protozoa, on the other hand, are ingested by the insect, and their moisture requirements are satisfied by the provisions of the insect's alimentary tract or body cavity" (Steinhaus, loc. cit.). This mode of invasion "imposes rather rigid tolerances in the environmental conditions which permit disease induction" (Roberts & Yendol, 1971), these limits being more strict than the requirements of other diseases. Young and, particularly, gregarious larvae are more prone to disease, as after initial infection its spread is largely dependent on host-density; in addition, hibernating caterpillars are especially at risk because of the accompanying seasonal moisture. Roberts & Yendol (loc. cit.) thought that fungal epizootics were "usually associated with periods of high humidity, particularly rainy periods". Other foreign ecologists were so certain of the connection that Steinhaus (loc. cit.) wrote, "The actual amount of rainfall has been used in prognosticating the probable success or failure of entomogenous fungi in naturally controlling certain insects". Furthermore, in some countries special agricultural techniques have been used to help keep a moist environment for the induction of fungal epizootics (Franz, loc. cit.); and Wilding (1981) mentioned that one particular insect species was only infected after monthly rainfall exceeded 20mm. Ullvett (1947) reported that a fungus attacked larvae of Plutella xylostella L. in South Africa when rain occurred, yielding high mortality rates; and Barrett (1882) had already postulated that as regards British lepidopterous larvae and pupae "mild winters act directly. . encouraging the growth of mould, which we know attacks them as soon as, from excess of rain or humidity, they become sickly". Despite the absence of reports of fungal disease within our butterfly at the time of its disappearances, modern experience with continental stock has apparently shown the presence of such a pathogen. Moreover, Martelli (loc. cit.) recorded that some A. crataegi were attacked by a fungus in Italy in 1928, although this was in the pupal stage. A hypothesis of a fungal epizootic being mainly responsible for the extinction of A. crataegi in this country dovetails into most of the known facts and thus answers almost every question.

Viruses

Heath (*loc. cit.*) suggested that the numbers of the black-veined white might have been heavily reduced by a virus disease. Although there is no direct evidence from this country, Hughes (1957) listed a bibliography of papers concerning insects which had been recorded

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as suffering from virus diseases anywhere in the world and such infections in *A. crataegi* have been noted in Italy, and in Germany from 1921 to 1924 (Steinhaus, 1967). Kreig & Lagenbuch (1956) mentioned that a polyhedral virus had been described many times within German *A. crataegi* larvae. High humidities, such as those brought about by rainy Septembers, could assist a catastrophic virus attack (Franz, *loc. cit.*). Steinhaus (1967) confirmed that certain virus diseases caused autumnal epizootics in America. However, the environmental conditions under which such outbreaks occur are not *essentially* associated with rainfall, as was mentioned under the previous heading, although the possibility remains.

(To be continued)

Notes and Observations

THE PAPERS OF J. O. WESTWOOD: OXFORD UNIVERSITY v. THE SMITHSONIAN INSTITUTION. – A contribution to the *Record* seldom causes an international controversy, but this writer's account of the collection of John O. Westwood's papers in the Smithsonian Institution Archives, Washington, D. C. (91: 245-246) achieved that dubious distinction. The affair is of concern because of the disturbing results of negotiations between the Smithsonian and Oxford University.

Although the Smithsonian's collection of Westwood's correspondence and manuscripts had been properly acquired in the nineteenth century, Oxford officials strenuously claimed it after noticing the 1979 *Record* account, arguing that the University was the holder of Westwood's papers (*recte*, the majority of them). The request appears to have been based on insufficient knowledge of the nature of archival collections and the historical realities of their distribution. Scholars and informed archivists know well that papers of individuals have often been divided and scattered through historical circumstance, accumulating in several or more repositories. Yet Oxford pressed its curious demands until the Smithsonian relented and gave up the collection. The ceremony of transfer was described in the Oxford *Times* (21 May 1982, p. 1).

One can understand the Smithsonian's desire to keep the peace between major institutions, but it and the University must share the blame for establishing such an unfortunate precedent. It is perhaps true that scholars might benefit by consulting both collections under one roof, but such convenience was not the issue in this debate. Apparently Oxford officials believed that another repository should 'stand and deliver' under the circumstances. But why should repository A give up its manuscripts to repository B when B has a larger collection of similar papers and demands A's holdings? Such a confrontation might have been more appropriate in the American Wild West or in the Essex countryside of Dick Turpin's time.

If small institutional collections of personal papers are to be claimed and acquired by the present holders of larger portions, the result will be unfortunate, to say the least. Many of us depend upon

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